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Aquatic Fungi

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1. Introduction

Seventy-one percent of our planet's surface consist of water, but only 0.6% are lentic and lotic freshwater habitats. Often taken for granted, freshwaters are immensely diverse habitats and host >10% of all animal and >35% of all vertebrate species worldwide. However, no other major components of global biodiversity are declining as fast and massively as freshwater species and ecosystems. Urbanisation, economic growth, and climate change have increased pressure on freshwater resources, whilst biodiversity has given way to the increasing demands of a growing human population. The adverse impacts on aquatic ecosystems include habitat fragmentation, eutrophication, habitat loss, and invasion of pathogenic as well as toxic species. Although there is increasing evidence that freshwater fungal diversity is high, the study of the biodiversity of freshwater fungi is still in its infancy. In light of the rapid decline in freshwater biodiversity, it is timely and necessary to increase our efforts to evaluate the diversity and potential ecological function of this fascinating and diverse group of freshwater organisms.

Hyde et al (2007) have estimated that there are approximately 1.5 million fungal species on earth. Of these, only around 3000 species are known to be associated with aquatic habitats and only 465 species occur in marine waters (Shearer et al., 2007). This small proportion of aquatic fungal taxa is surprising because the aquatic environment is a potentially good habitat for many species. Based on this notion we assume that the "real" number of aquatic fungi is much larger than 3000 and includes a large variety of hitherto undescribed species with unknown ecological function.

Aquatic fungi are usually microscopic organisms, which do not produce visible fruiting bodies but grow asexually (anamorphic fungi). Their occurrence in water is rather subtle and specialised methods are needed to examine their diversity, population structure and ecological function. Water associated fungi have been known historically as "phycomycetes", a functionally defined group consisting of "true fungi" (*Eumycota*) and "analogously evolved fungus-like organisms" belonging to *Chromista* (*Oomycetes*, *Thraustochytridiomycetes*). Other groups formerly placed in the fungal kingdom include slime moulds (*Amobae*), *Ichthyosporae (Mesomycetozoea)* and *Actinomycetes (Bacteria)*, which are now recognised as distinct taxa. While the "true fungi" are a sister group to animals, *Oomycetes* are biochemically distinct from fungi while having similar morphology, size and habitat usage (Money, 1998). Colloquially known as "water moulds", they comprise approx. 200 species inhabiting freshwater, mud and soil. Many of these are saprobes or parasites

(Czeczuga et al., 2005; Nechwatal et al., 2008). Slime moulds (*Amoebozoa*; Adl et al., 2005) are also found in freshwater habitats. Although they are relatively easy to isolate from plant detritus submerged in ponds and lakes, their ecology is little known and requires further investigation (Lindley et al., 2007).

Aquatic "true fungi" are osmoorganotrophs, absorbing nutrients across their cell wall. Most of them have a filamentous growth stage during their life cycle. This morphology enables them to invade deep into substrates and to directly digest particulate organic matter (POM) to acquire nutrients for growth and reproduction. Fungal filaments vary in length from several micrometers for the "rhizoids" of *Chytridiomycetes* to several millimetres or metres for hyphae or hyphal networks, e.g. of hyphomycetes colonising leaves, wood, and soil. However, there are always exceptions, such as unicellular yeasts, which lost filamentous growth during their evolution. Here, we will focus on diversity and function of fungi in various aquatic systems.

1.1 Characteristics of the aquatic habitats influencing fungal life

Aquatic habitats are characterised by a unique balance of allochthonous (external) and autochthonous (internal) organic matter supply, which is controlled largely by watershed characteristics, surface area and location. For example, headwater streams and small ponds receive most of their organic matter from terrestrial riparian vegetation, whereas large lakes are mainly supplied with organic matter internally from algal primary producers. Organic carbon derived from terrestrial vegetation varies substantially from that of algae. Plant remains contain large fractions of lignin, hemicelluloses and cellulose, which prolong microbial decomposition to several months, whereas algae contain much fewer recalcitrant polymers and thus are rapidly mineralised, usually within a few days. In small or shallow lentic systems submerged and emergent aquatic macrophytes often dominate the primary production, representing the most productive non-marine ecosystem worldwide. Aquatic fungi, being heterotrophs, are reliant upon photosynthetically produced organic matter. In order of decreasing biodegradability, the fungal community consumes microscopic algae, macroscopic aquatic macrophytes and terrestrial plant litter (including wood). On localised spatial scales or short-term temporal scales, carbon and nutrients from other sources may gain high importance. Resources derived from animals include fish, fish eggs, carcasses, excuviae, living zooplankton, insects, feathers and hair, while other plant-derived resources include pollen, spores, seeds and fruits (Cole et al., 1990). Interestingly, it seems to be nearly impossible to find a natural organic source that cannot be utilized by aquatic fungi (Sparrow, 1960). This notion points to either a high functional redundancy of a limited set of fungal species or to a high biodiversity of fungal specialists. Most likely, in natural systems both cases occur at the same time. Another interesting feature of aquatic habitats is the coupling of aquatic systems to terrestrial environments via animals, mainly insects, which are able to export nutrients from the aquatic ecosystem (Vander Zanden & Gratton, 2011). It will be shown later, that fungi are often closely associated with insects, which can be key organisms in aquatic freshwater systems. Although often overlooked, fungi represent a common and important component of almost every trophic level of any aquatic ecosystem.

2. Life styles of aquatic fungi

Aquatic habitats are heterogeneous in time and space and greatly differ in their physico-chemical features. Consequently, composition and abundance of aquatic fungi should differ

significantly between these habitats (Wurzbacher et al., 2010). Whereas Wurzbacher et al. (2010) have recently reviewed the ecology of fungi in lake ecosystems, and present a thorough discussion on fungal communities within the different water bodies, in this book chapter we want to present a concise overview on fungal life-forms and diversity in various water bodies.

2.1 The role of fungi as decomposers, predators, endophytes, symbionts, parasites, plagues & pathogens

Aquatic fungi are heterotrophs, i.e. they *sensu stricto* depend on external organic matter, which may be dead or alive. Aquatic systems harbour a wealth of organisms that can serve as suitable hosts: algae from different phyla, cyanobacteria, protists, zooplankton, fish, birds, mussels, nematodes, crayfish, mites, insects, amphibians, mammals, plants and other fungi (Sparrow, 1960; Ellis & Ellis, 1985). Fungi are omnipresent and therefore associated with almost every organism, often as parasites, sometimes as symbionts and of course as decomposers.

Parallel to fungi in soil, aquatic fungi act as prominent decomposers of POM: foremost coarse particulate organic matter (CPOM) including plant and animal debris. Filamentous growth habit is a key feature of many aquatic fungi, and this feature is responsible for their superiority to heterotrophic bacteria as pioneer colonisers. Hyphae allow fungi to actively penetrate plant tissues and tap internal nutrients. Therefore, Gessner & Van Ryckegem (2003) describe fungal hyphae as self-extending digestive tracts that have been turned inside out growing hidden inside the substrate.

The aquatic fungi which typically decompose leaf litter and wood with a hyphal network are the polyphyletic group known as "aquatic hyphomycetes". Aquatic hyphomycetes are most common in clean, well oxygenated, flowing waters (Ingold, 1975; Bärlocher, 1992), and are characterised as anamorphic fungi with tetraradiate or sigmoid conidia (asexual reproductive structures). Taxonomically, they are mainly associated with the *Ascomycota*, and only a small percentage is affiliated with the *Basidiomycota*. In contrast, aero-aquatic hyphomycetes colonise submerged plant detritus in stagnant and slow flowing waters, such as shallow ponds and water-filled depressions. Taxonomically, most aero-aquatic fungi are classified as *Ascomycota*, although four aero-aquatic species have been classified as *Basidiomycota*, and one as O*omycete* (Shearer et al., 2007). These fungi are adapted to habitats with fluctuating water levels subjected to periodic drying, low levels of dissolved oxygen, and elevated levels of sulfide. Therefore, they have buoyant conidia that are released at the water surface as water levels recede. Along with aquatic fungi, terrestrial fungi enter the aquatic realm as pioneer decomposers and endophytes of allochthonous plant debris. In the water, however, they are partially replaced by true aquatic hyphomycetes. After colonising the substrate and forming internal hyphal networks, the POM is macerated at least partly by the fungi themselves. This process is often accelerated by the feeding activity of macroinvertebrates, which find colonised leaves to be more palatable (compiled in Bärlocher, 1992; Gessner & Van Ryckegem, 2003). With the aid of an array of extracellular enzymes, aquatic fungi are able to degrade most of the polymeric substances in leaves (hemicelluloses, cellulose, starch, pectin and to some extent lignin; Krauss et al., 2011). Depending on leaf litter type and water chemistry, fungal leaf decomposition can extend over 1 to 6 months. The situation is slightly different for fungal decomposition of emergent macrophytes, because decomposition starts in standing shoots. Over 600 species of fungi have been recorded from the litter of *Phragmites australis* alone (Gessner & Van Ryckegem, 2003). Ninety four percent of these 600 species were members of *Ascomycota* and only 6%

belonged to *Basidiomycota*. The *Ascomycota*, in turn, comprised 30% aquatic hyphomycetes (with "naked" conidia) and 22% coelomycetous anamorphs (producing conidia inside a fruiting body). Thirty species isolated from the standing dead shoots of *Juncus effusus* (Kuehn & Suberkropp, 1998) were also mainly composed of aquatic hyphomycetes and coelomycetes. White rot *Basidiomycetes*, generally not considered being active in aquatic habitats, have also been isolated from standing dead aerial shoots in wetlands. In the case of small particles such as algae, pollen, seeds and zooplankton carcasses, decomposition is achieved by the much smaller *Oomycetes* and *Chytridiomycetes*, rather than the aquatic hyphomyctes. These organisms do not depend on macro-scale hyphal networks and are capable of very fast responses to changes in their environment. Their motile spores actively search for adequate substrates using chemotaxis. Once a suitable substrate has been reached, an appressorium is formed and the particle is invaded by tiny rhizoids tapping the internal nutrient reservoirs for production of new spores in a sporangium (either endo- or ectophytic; Sparrow, 1960; Sparrow, 1968 and references therein). Thereby, their whole life cycle can be completed in days. The short generation times and prolific spore production characterise these fungi as typical r-strategists.

Another polyphyletic group of aquatic fungi (with members of *Oomycetes, Zoopagomycotina* and *Basidiomycetes*) is specialised to hunt by using traps. These predatory fungi are often found on decomposing plant material or animal egesta. They use sticky traps, networks or slings to entrap their prey, usually amobae, rotifers, nematodes, liver flukes and small arthropods like mites. After the prey is caught, these fungi penetrate the prey's tissue and digest it from the inside. Generally, it is assumed that this behaviour supplies these fungi with additional nutrition when colonizing decomposing plant detritus. In soil, additional groups of endoparasitic fungi are found, e.g. on nematodes (Family *Hyalosporae* & *Entomophthoraceae*) which also destroy their prey from the inside (Karling, 1936; Drechsler, 1941; Peach, 1950, 1952, 1954; Sparrow, 1960; Swe et al., 2008).

An additional strategy of fungi with presumably long annual life cycles, is to grow inside living plants without affecting the host's viability. Yet, it is unclear whether the host plant benefits from these "endophytes" or if the relationship between plant and fungi is solely based on commensalism. Obviously, when the host plant enters senescence, all internal fungi have a great advantage over the secondary colonising fungi since the primary rule of "first come, first serve" is of major importance for growth and reproductive success.

An important group of endophytic fungi, which is clearly beneficial for the plant, consists of mycorrhiza forming symbionts present in the roots of several aquatic macrophytes. Many mycorrhiza forming symbionts belong to a phylum of the "lower fungi" called *Glomeromycota*. Certain orders of the *Glomeromycota* are obligate root symbionts characterized by a vesicular arbuscular mycorrhiza (VAM) that supply their hosts with nutrients. In return, the host plant provides the fungus with sugars rich in energy, amongst other things. VAM fungi were formerly believed to be purely terrestrial, but today it is known that they are particularly important in nutrient poor clear waters. For example, in oligotrophic waters, VAM fungi allow macrophytes to grow under nutrient limiting conditions by supplying the plant with solid-phase bound nutrients (Baar et al., 2011).

Freshwater algae, e.g. *Dunaliella* and the autotrophic protozoan *Euglena* can establish a mutual relationship with the fungus *Bispora* or the yeast *Cryptococcus,* respectively (Gimmler, 2001). Moreover, fungi belonging to the *Kickxellomycotina* are endosymbionts of invertebrates, especially of aquatic arthropods and - together with specialised protozoans - are summarised under the term trichomycetes (Lichtwardt, 2004; Hibbett et al., 2007).

A cornerstone of fungal lifestyle is parasitism. The life cycle of parasitic fungi is identical to that of saprophytic fungi with one exception: the host cells are still alive. Therefore, it is often impossible to separate opportunistic fungi colonizing senescent hosts from the true parasitic fungi reducing the fitness and in some cases even causing death to their previously healthy hosts. Prominent aquatic parasitic fungi belong to *Chytridiomycota* and *Oomycetes*. The host spectrum of these aquatic fungi is broad and covers every phylum including fungi itself (Sparrow, 1960; Van Donk & Bruning, 1992; Ibelings et al., 2004; Kagami et al., 2007). Encounters with fungi can be fatal to algae, particularly if their defence system is breached by the fungus. The ecological relevance of this negative interaction becomes evident when it is considered that suicide is a common defence mechanism in algae. If this controlled progress, called hypersensitivity, is initiated at the right moment during fungal infection, it results in the successful interruption of the fungal infection cycle, because the parasite's ability to reproduce via spore production is inhibited. Such "behaviour" allegorises a beneficial sanction since it protects the healthy algal population by reducing the abundance of the deadly parasite. However, if unsuccessful the parasite prevails and mass mortality of algae results. This can lead to shifts in the algal community composition.

In rare, but important cases, fungi cause severe damage to larger aquatic organisms. Some fungi, mainly but not exclusively *Oomycetes*, infect fishes or fish eggs (Noga, 1993; Chukanhom & Hatai, 2004) and thereby exert strong population pressure. This is of great importance for aquaculture since it necessitates antifungal treatments, but even in natural systems, fungi have the potential to severely harm the indigenous fish population. *Aphanomyces astaci* (*Oomycetales*) causing the crayfish plague has driven the European crayfish (family *Astacidea*) population to the edge of extinction (Reynolds, 1988). In contrast, *Coelomomyces* (*Blastocladiomycota*) effectively infecting several mosquito species (Sparrow, 1960) has been discussed as a biological control for malaria mosquitoes (Whisler et al., 1975). The most infamous fungal parasite is *Batrachochytrium dendrobatidis* (*Chytridiomycetales*), which contributes to worldwide extinction of several known and unknown amphibian species (Berger et al., 1998; Skerratt et al., 2007). Aquatic plants are also greatly affected by fungal parasites. A recently discovered plant parasite is *Pythium phragmites* (*Oomycetales*), obviously being an important causative agent of reed decline (Nechwatal et al., 2005).

Some human pathogens may also be found amongst the aquatic fungi. Common freshwater yeasts belonging to *Candida* and *Cryptococcus* are both potentially harmful to humans (e.g. *C. albicans* and *C. tropicalis*). These fungi are frequently found along bathing sites (Vogel et al., 2007). Several typical dermatophytes and keratinophylic fungi are transferred via water and can also occur in aquatic ecosystems (Ali-Shtayeh et al., 2002). *Chytridiomycetes* and "Microsporidia", however, are rarely pathogenic and only infect immune-deficient patients. Additionally, black yeasts are on occasion salt-tolerant and thus can cause problems when consuming salt preserved food (Butinar et al., 2005).

2.2 The life cycles of aquatic fungi

Life cycles of aquatic fungi cover a broad spectrum from very simple cell divisions to very complex cycles, crossing the terrestrial-water boundary. Starting with basal fungal lineages, Microsporidia are intracellular parasites with an extremely reduced genome (down to 2.3 Mbp, which is half the genome size of the common enterobacterium *Escherichia coli*). They are transmitted passively with non-motile spores, which have a size range of 1 - 50 µm. Endospores are chitinous and mature inside host-cells, where they are eventually released by an extrusion apparatus (summarised by Keeling & Fast, 2002).

Members of "Rozellida" have a similar life cycle as *Chytridiomycetes*, although diversity of *Rozella* has been so far only marginally described and is mainly based on the description of *Rozella allomyces*, a parasite living on *Allomyces sp.* The environmental clade LKM11 (van Hannen et al., 1999), the other member of Rozellida, is so far completely undescribed with scarce information about its habitat and ecology. It is known that these organisms probably have zoospores in the size range of 0.2 – 5 μm, which are most abundant above lake sediments (Mangot et al., 2009). They are also found under reduced oxygen and anoxic conditions, (Slapeta et al., 2005; Luo et al., 2005). Under anoxic conditions potential relatives of the *Neocallimastigomycota*, an obligate anaerobic symbiotic group of ruminants can be found, too (Lockhart et al., 2006; Mohamed & Martiny, 2011). However, their life cycle is similar to that of the *Chytridiomycetes*. Briefly, a zoospore is chemically attracted to its host or substrate and attaches to its surface. Then a cyst forms and tiny rhizoids (or a penetration tube) grow into the substrate to gather nutrients for (endobiotic or epibiotic) sporangium formation. Thereafter, masses of zoospores can be discharged (up to 70 000 for *Rhizophlyctis petersenii*). Sexual recombination can occur when two zoospores fuse together either in the free-swimming stage or on the host/substrate surface. Alternatively, resting spores might be formed in a prosporangium or in a zygote (Sparrow, 1960).

In principle, the life cycle of *Blastocladiomycota* is quite similar to that of the *Chytridiomycetes*, although they have hyphal growth in addition to zoospores. An important group within the *Blastocladiomycota* is comprised of members of the *Coelomomycetes*, which are often species-specific for their mosquito host. Their complete life cycle, originally described by Whisler et al. (1975), is given in figure 1.

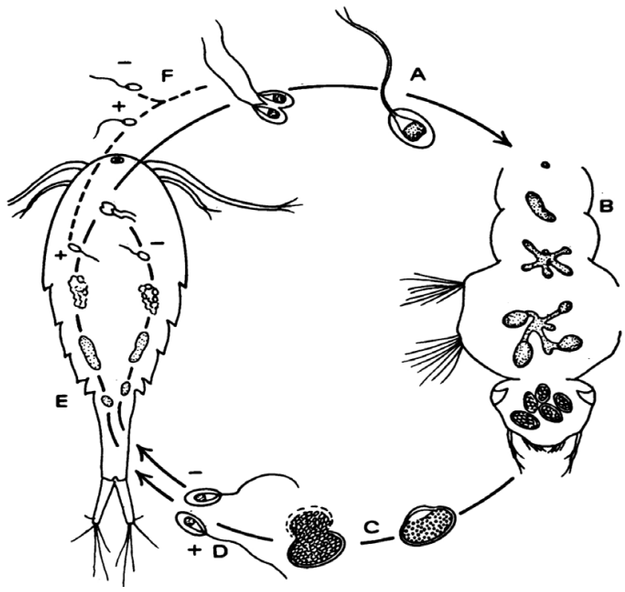

Fig. 1. Life cycle of *Coelomomyces psorophorae*. Zygote (A) infects larva of *Culiseta inornata* (B) leading to development of hyphal bodies, mycelium and, ultimately, thick-walled resistant sporangia. Under appropriate conditions these sporangia (C) release zoospores of opposite mating type (D) which infect the alternate host, *Cyclops vernalis* (E). Each zoospore develops into a thallus and, eventually, gametangia. Gametes of opposite mating type (F) fuse either in or outside of the copepod to form the mosquito-infecting zygote (Whisler et al., 1975, with permission).

Mosquitoes, like other arthropods, are potential hosts for symbiotic trichomycetes (*Harpellales)* in many lentic and lotic freshwater habitats (Lichtwardt, 2004; Koontz, 2006; Strongman & White, 2008). These gut fungi disperse via trichospores through the water column.

Parasitic members of *Entomophthorales* also use arthropods as hosts. In insects with aquatic and terrestrial life stages, these parasites are well adapted to both habitats by developing asexual conidia for dispersal in air and typical tetraradiate conidia for dispersal in water. A detailed description has been given by Hywel-Jones & Webster (1986) and is depicted in figure 2. The idea of a second host is especially inspiring, since it is known that *Entomophthorales* are also parasites of planktonic desmids (green algae; Sparrow, 1960).

Leaf decomposition is associated with high discharges of aquatic conidia of diverse shapes and sizes (e.g. Ingold, 1975), although the conidia of aquatic hyphomycetes are typically tetraradiate. Aquatic hyphomycetes reproduce asexually (figure 3), although in ca. 10 percent of all described species, teleomorphs have been found, e.g. on twigs at river margins (Webster, 1992).

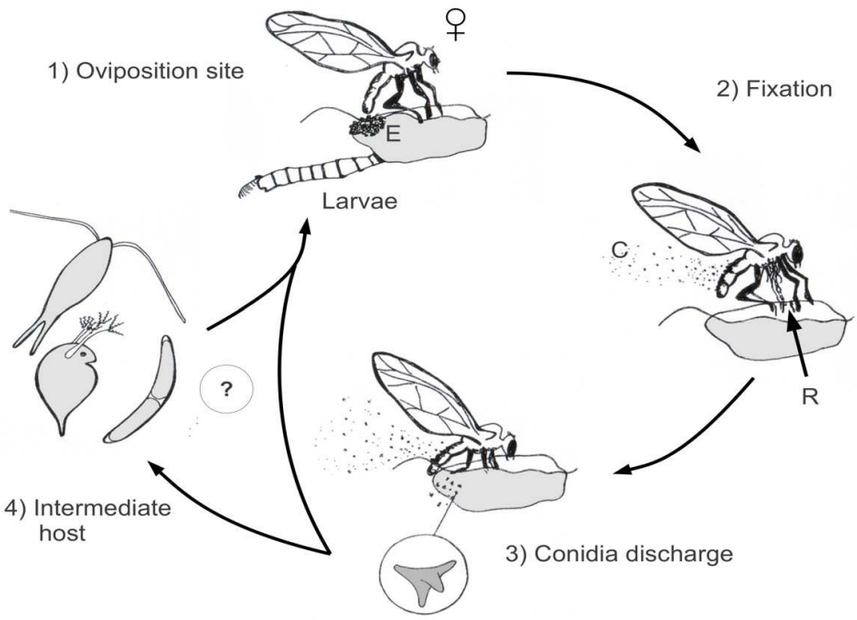

Fig. 2. Life cycle of *Erynia conica* on *Simulium sp.* (1) After oviposition (E), only infected females of *Simulium* stay at the river bank and become less active. (2) After 2-12 hrs, rhizoids (R) and pseudocystidia emerge from small swellings at the abdomen. The rhizoids anchor the animal to the ground and inhibit any further locomotion. After 15 hrs, conidiophores and primary aerial conidia emerge (C) and release. (3) After 24 hrs, when the ventral part of the fly is wetted or submerged, primary aquatic conidia are produced. Both types of conidia can be produced simultaneously in a single fly for up to 96 hrs after arrival at the oviposition site. Globose zygospores, however, stay embedded in the cadaver (teleomorphic form). (4) Aerial conidia can transform into secondary stellate aquatic conidia with typical tetraradiate symmetry upon submersion. Yet, it is not clear whether secondary hosts (zooplankton or desmids) are required for *Erynia* development because aquatic conidia were never observed to cause infection of *Simulium* (Webster 1992). Illustration drafted after descriptions of Hywel-Jones & Webster (1986).

Other filamentous fungi, such as endophytes or VAM fungi have a still more or less unknown life cycle. Though, it is similar to *Mucor* species in sediments, an interesting phenomenon occurs in this genus, which may be relevant to other fungi with yeast-like life stages. While *Mucor* usually grows in hyphal networks when oxygen is available, under certain circumstances (especially when growing anaerobically, at elevated pCO_2), growth changes to a yeast-like morphology (Orlowski, 1991). This dimorphism is known of several yeast-like species such as *Aureobasidium pullulans* or *Candida* sp. and triggers a fast adaptation to changing environmental conditions. Yeasts and yeast-like organisms have often been isolated from freshwaters, a habitat varying greatly in time and space. For example, waves, chemical gradients and currents may be highly variable over time and hence, the capability to adapt rapidly to such changes is of great advantage.

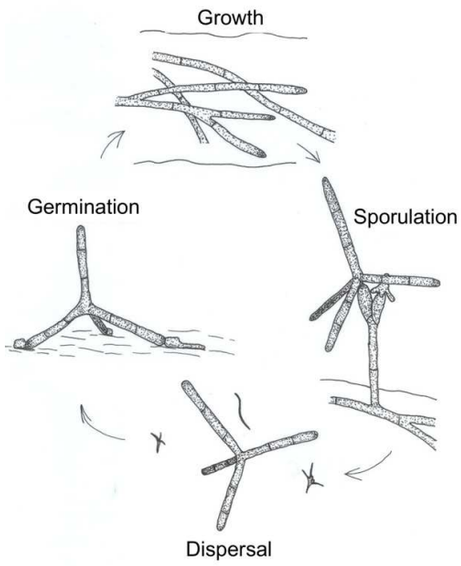

Fig. 3. Asexual life cycle of aquatic hyphomycetes. Figure reproduced from Gulis et al. (2009) with permission.

2.3 Differences in fungal morphology and ecology

Fungi can grow into the largest known organism on earth if the substrate is suitable and the environmental conditions favourable. In most cases, however, fungi remain invisible to the naked eye. Therefore, their global importance is seldom recognised even by scientists. Fungi literally tend to grow to the limit of their natural potential; the size of their cellular network is not genetically encoded, but defined by substrate and other environmental parameters. If, in the very unlikely event that a scientist attempted to prove that a whale could survive in freshwater, the whale's inevitable death would be rapidly followed by colonization of the gigantic carcass by coprophilus fungal species (as observed for various fish carcasses; Fenoglio et al., 2009). These fungi would flourish throughout the decomposition of the carcass and a single species could potentially establish an extensive network, exploiting a substantial portion of the whale's biomass. Most likely, the whale's carcass would harbour a very diverse fungal flora of several phyla and hundreds of species, supporting a whole benthic food web with nutrients and energy for years. In contrast, tiny substrates such as single celled diatoms of a few µm in

diameter, only harbour a single fungal species with an evanescent low biomass. However, taking the size of a large water body and the high annual abundance of diatoms into account, the fungal biomass associated with these algae could exceed those growing within the whale carcass. Thus, substrate size is not the sole factor determining the importance of aquatic fungi in their natural habitat.

Aside from their dependence on substrate quality and quantity, fungi themselves harbour different morphologies, life stages and strategies. This is mainly due to the fact that aquatic fungi are derived from many fungal phyla comprising different cellular "blueprints" and life stages (see above). The diameter of a single fungal cell can roughly vary within an order of magnitude and there are numerous different spore morphologies extending from 1 µm small flagellated zoospores to several 100 µm large air-trapping conidia. An overview of fungal dimensions in aquatic systems is shown in figure 4.

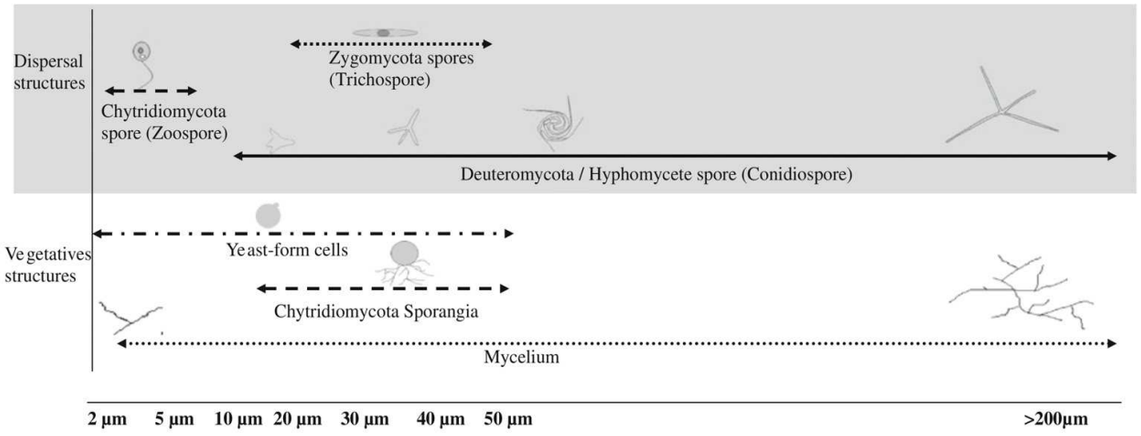

Fig. 4. Dimensions of vegetative growth forms and spores of aquatic fungi (republished from Jobard et al., 2010, with permission).

2.4 Diversity in large-scale aquatic habitats

Many aquatic fungi are saprophytes, which consume dead organic matter (Dodds, 2002), but aquatic fungi may also be parasites or symbionts. In aquatic systems, the fungal community structure greatly differs between substrates (Shearer and Webster, 1985; Findlay et al., 1990; Bärlocher & Graça, 2002; Graça et al., 2002; Mille-Lindblom et al., 2006) and with the physico-chemical properties of the respective habitats, such as flow (Pattee & Chergui, 1995; Baldy et al., 2002), dissolved oxygen concentration (Field & Webster, 1983; Medeiros et al., 2009), nutrient concentrations (Gulis & Suberkropp, 2004; Rankovic, 2005), salinity (Hyde & Lee, 1995; Roache et al., 2006), temperature (Bärlocher et al., 2008) and depth (Wurzbacher et al., 2010). Therefore, fungal communities potentially differ between streams, shallow lakes and wetlands, deep lakes, and other habitats such as salt lakes and estuaries.

2.4.1 Fungal diversity in streams

Upland stream habitats are characterised by a pool and riffle structure with relatively swift flow and high levels of dissolved oxygen. These streams are narrow and tend to be lined by overhanging riparian vegetation. These characteristics create an ideal habitat for aquatic hyphomycetes. Nikolcheva & Bärlocher (2004) have investigated the structure of fungal

communities on leaves submerged in an upland stream by using molecular methods. The authors were able to resolve the diversity within the *Ascomycota, Basidiomycota, Chytridiomycota, Zygomycetes* and *Oomycetes* and found, that the leaf decomposer community was dominated by *Ascomycota*, whereas *Basidiomycota* comprised a small but consistent fraction of aquatic fungi. *Chytridiomycota* represented a substantial proportion of the fungal community in winter, while *Oomycetes* were only present in summer. *Glomeromycota*, however, were of minor importance in the stream environment. Species common in an Australian upland stream included *Tetrachaetum elegans*, *Lunulospora cymbiformis*, *Flagellospora penicillioides* and *Alatospora acuminata* (Thomas et al., 1992). These species of aquatic hyphomycetes have not yet been associated with a teleomorph, but are likely affiliated with the *Ascomycota* since they lack morhpological features characteristic of the *Basidiomycota* (Nawawi 1985).

In lowland rivers, flow remains substantial but water quality and the source of primary production are substantially different from those in upland streams. Wider channels lead to a proportional reduction in litter from riparian plants, and production from phytoplankton is of increased significance (Vannote et al., 1980). Nutrient concentrations and dissolved organic carbon may also be higher, leading to lower or fluctuating concentrations of dissolved oxygen. Thus, while aquatic hyphomycetes still dominate submerged litter in these streams (Baldy et al., 2002), fungal community composition differs from upland streams (Shearer & Webster, 1985) and biomass accumulation may be limited by competition with other microorganisms, substrate burial and lower oxygen availability (Bärlocher, 1992; Medeiros et al., 2009).

2.4.2 Fungal diversity in shallow lakes and wetlands

The dominant fungi colonising submerged plant litter in shallow, stagnant habitats common in wetlands and shallow lakes are the aero-aquatic hyphomycetes (Glen-Bott, 1951; Shearer et al., 2007). On occasion, aero-aquatic hyphomycetes may be found in streams and aquatic hyphomycetes in wetlands (Bärlocher & Kendrick, 1974; Fisher et al., 1983; Bärlocher, 1992), but aero-aquatic hyphomycetes are capable of out-competing aquatic hyphomycetes when colonising substrates in water with lower oxygen or higher nutrient concentrations (Voronin, 1997). *Oomycetes* and terrestrial fungi can also be found in wetlands (Bärlocher, 1992).

Fungal genera commonly found in wetlands include *Alternaria, Cylindrocarpon, Cladosporium, Penicillium, Fusarium, Trichoderma* and aquatic hyphomycetes (*Alatospora, Tetracladium, Helicodendron, Helicoon*; Kaushik & Hynes, 1971; Kjoller & Struwe, 1980; Ford, 1993). Aquatic lichens (a symbiotic partnership between a fungus and an alga) are potentially present in the littoral zone of wetlands, lakes and streams (McCarthy & Johnson, 1997), in particular in temperate or boreal regions (Hawksworth, 2000). There are ca. 200 species of lichenised fungi known from freshwater systems (Hawksworth, 2000). The main orders of *Oomycetes* found in aquatic environments are the *Leptomitales*, *Saprolegniales* and *Peronosporales*. Their requirement for dissolved oxygen varies widely among species, and many are intolerant of high salinity (Dick & Newby, 1961; Dick 1962; 1963; 1969; 1972).

2.4.3 Fungal diversity in deep lakes and reservoirs

In deep lakes and reservoirs, the abundance (as colony forming units; CFU) and diversity of aquatic fungi is greatest in both the littoral and profundal zone (Rankovic, 2005).

Considering filamentous and higher fungi, the pelagic zone only supports a few specialised fungal species, but seems to be mainly used as a medium for propagules dispersal (Wurzbacher et al., 2010). Fungi from the littoral zone, in turn, are saprobes, parasites, predators, endosymbionts or occasionally lichens. These organisms colonise substrates ranging from submerged plants and litter to the carapaces of dead micro-crustaceans (Czeczuga et al., 2002; 2004; 2007).

In the pelagic zone, fungi consist mainly of species that live parasitically on phytoplankton, zooplankton and fish. Taxonomically, the fungal community consists of *Ascomycete* and *Basidiomycete* yeasts and "zoosporic fungi" (*Chytridiomycota* and *Oomycetes*; Rankovic 2005; Lefevre et al., 2007). It has been suggested that "zoosporic fungi" and their propagules are important for pelagic food web dynamics since they are important parasites of freshwater algae and thus may be important in controlling phytoplankton blooms associated with diatoms (Kagami et al., 2004) and cyanobacteria (*Microcystis* spp.; Chen et al., 2010).

The profundal zone and lake sediments, however, mainly serve as a propagule bank, where resting spores are stored. Therefore, both aquatic and terrestrial species are frequently isolated from deep lake sediments. Moreover, it has been suggested that yeasts in lake sediments are derived from terrestrial plant litter (Kurtzman & Fell, 2004), and fungal CFU associated with the *Mucoromycotina* (*Mucor* and *Rhizopus* sp.) isolated from various Serbian reservoirs may be also of terrestrial origin (Rankovic, 2005). However, there are a few species of yeasts, *Chytridiomycetes* and *Oomycetes* that are able to grow vegetatively in lake sediments (e.g. Ali & Abdel–Raheem, 2003).

2.4.4 Other aquatic habitats

Fungi may also be found in aquatic habitats with harsh environmental conditions, such as sulfidic springs (Luo et al., 2005), acidic peat bogs and lakes (Thormann, 2006; Voronin, 2010) and volcanic lakes (Sabetta, et al., 2000). When studying fungal diversity in sediments of an estuary, Mohamed & Martiny (2011) found that community composition (at division level) did not differ substantially between fresh, brackish and seawater. However, the proportion of *Chytridiomycetes* and unknown species from basal lineages increased with salinity, and species diversity was at a maximum in the brackish zone. Although several studies have examined the fungi that can be isolated from saline lakes (Butinars et al., 2005; Zalar et al., 2005; Takishita et al., 2007) and mangroves (Suryanarayanand & Kumaresan, 2000; Kumaresan & Suryanarayanan, 2001; Ananda & Sridhar, 2002), fungal biodiversity in these systems requires further investigation.

3. Hidden biodiversity of aquatic fungi

Actual fungal biodiversity suggests that the most species-rich regions of the globe are situated in temperate rather than in tropical regions. Given that many fungal species are host or substrate specific, and that biodiversity of plants and animals is highest in tropical regions, this notion is counter-intuitive. It is very likely that sampling efforts for fungal biodiversity have been largely restricted to temperate regions, where most fungal taxonomists are situated (Shearer et al., 2007). Alternatively, seasons, cooler temperatures and moist conditions may be more amenable to fungal evolution and niche differentiation. From the above mentioned discrepancies and gaps of knowledge in diversity of aquatic fungi, it appears timely to commence co-ordinated world-wide

sampling programs using consistent methodology to evaluate fungal biodiversity in various aquatic systems around the globe.

Gessner & Van Ryckegem (2003) estimated the total number of aquatic fungal species to a maximum of 20 000 different species based on the assumption that only 5% have been described so far. Whereas only a few newly described fungal species have been added in recent years, an increasing number of genetically distant environmental DNA sequences have been found (Hibbett et al., 2011). For example, biodiversity of basal fungal lineages, which bear numerous aquatic species, seems to be much higher than expected. In addition, biodiversity of these basal phyla is elevated in aquatic sediments when compared to terrestrial soil (Mohamed & Martiny, 2011). The highest estimates of global fungal diversity reach up to 5 million species (Blackwell, 2011). The above mentioned "lower fungi" belonging to *Eumycota*, excluding congruously *Oomycetes* and *Thaustrochytrids*, are listed in table 1.

Currently, the species ratio of terrestrial fungi to land plants is approximately 10.6:1. Most likely, this ratio will increase in the future since mycologists have largely increased their efforts to find new fungal species. Freshwater ecosystems can be considered as rather unexplored fungal habitats whereby the few, presently available molecular studies point to a high species diversity. Blackwell (2011) gives helpful suggestions on where to search for these hidden species and highlights insects and other animals as potential fungal habitats. For example, in a single pilot-study in 2005, Suh et al. have isolated 196 new yeast species from guts of mushroom eating beetles and thereby increased the total number of worldwide described yeast species by more than 30%. Next to fungi residing in arthropod guts, endophytes in freshwater ecosystems are another budding source of high fungal biodiversity. For example, when applying molecular tools Neubert et al. (2006) found >600 fungal operational taxonomic units (a measurement of environmental DNA sequence diversity) in single plants (*Phragmites australis*) of a single lake (Lake Constance). This remarkably high diversity of endo- and ectophytic fungi points to a so far largely hidden fungal diversity associated with higher aquatic organisms.

As already mentioned, fungal parasites in pelagic systems can greatly add to global fungal diversity, which should by far exceed even that of saprophytic fungi. This is due to the following features of parasitic fungi: (1) the presence of a specialised attack-defence co-evolution based on the red queen hypothesis and (2) a high specificity to host species of various eukaryotes. A precise estimation of their diversity is difficult since parasites can be either host strain specific (De Bruin et al., 2008) or cover a wider spectrum of hosts such as *B. dendrobatidis.* In addition to parasitic fungi, many opportunistic saprophytic fungi are host-specific (Sparrow, 1960). Nevertheless, variability in host and substrate specificity is high among aquatic fungi and it is difficult to generalise.

3.1 Hidden diversity

Several aquatic microhabitats – well studied for bacteria - have not yet been well incorporated in biodiversity studies on fungi (Wurzbacher et al., 2010). These microhabitats include biofilms (periphyton, benthic algae), floating algae, and submerged/floating macrophytes, which contribute substantially to lake primary productivity. Detrital aggregates (lake and riverine snow) are also known hotspots of bacterial activity in the pelagic zone of lakes and large rivers, but fungal contribution to these aggregates has not been evaluated. Although remineralisation processes have been well studied for bacteria, fungi have been largely excluded from these studies. The riparian/littoral zone of aquatic

Phyla	Representatives	Known Hosts	Known Substrates	Remarks
Microsporidia*	*Glugea* *Telohania* *Pleistophora*	animals (incl. protists and zooplankton)		obligate endoparasites esp. of fishes and arthropods
Rozellida*	*Rozella* *LKM11*	fungi		obligate mycoparasites, common at anoxic sites
Chytridiomycota	*Rhizophydium* *Endochytrium* *Batrachochytrium*	mycoplankton, phytoplankton, zooplankton, animals, macrophytes	phytoplankton, zooplankton, animals, plant debris, seeds, pollen, fruits, chitin, keratin, cellulose, twigs	obligate and opportunistic endoparasites & ectoparasites; saprophytes
Neocallimastigo-mycota	*Piromyces*	ruminant	cellulose	obligate anaerobe symbionts, potentially in sediments
Blastocladiomycota	*Coelomomyces* *Catenomyces*	insect larvae, eggs of liver fluke, nematodes, aquatic fungi	fruits, twigs, animal debris	endoparasites of malaria mosquito Anopheles
Glomeroycota	*Glomus*	roots of aquatic macrophytes		obligate VAM building symbionts
Subphyla of Glomeromycota				
Mucoromycotina	*Mucor*		debris	fermentative metabolism possible
Entomophthoro-mycotina	*Ancylistes* *Macrobiotophthora* *Erynia*	insects, desmids, rotifers, nematodes	vegetable debris, excrements of amphibians	endoparasites & saprophytes
Zoopagomycotina	*Zoophagus*	amoebae, rotifers, nematodes, fungi (e.g. Mucor)		endoparasites & ectoparasites or predatory fungi
Kickxellomycotina	*Harpellales*	arthropods (e.g. Chironomidae)		coprophilous species and trichomycetes (symbionts of aquatic arthropods)

Table 1. Lower fungal phyla of *Eumycota* in accordance to Hibbett et al. (2007) and Lara et al. (2010). Detailed information was obtained mainly from Sparrow (1960), Hywel-Jones & Webster (1986), Ebert (1995), Keeling & Fast (2002), Lichtwardt (2004) and Benny (2009). Asterisks mark not yet confirmed phyla.

systems is an ideal habitat for fungi and hence should be the focus of future fungal biodiversity research. Littoral food webs are very complex and a wealth of invertebrates, vertebrates and progeny suggest close interaction with a diverse community of fungi including parasitic, symbiotic and endophytic fungi. Littoral zones are highly structured by large emerged macrophytes, floating macrophytes and submerged macrophytes, which can

form a dense meadow and are suitable habitats for fungal proliferation. The high diversity of algae, pelagic and benthic species, and their function as an accumulation zone for dissolved nutrients and terrigenous detritus from the catchment, renders the littoral zone an ideal fungal habitat. Littoral sediments are often well aerated by the roots of emergent and submerged macrophytes and form microenvironments with strong physico-chemical gradients frequently altered by water movement and bioturbation by invertebrates such as mussels or chironomids. Therefore, it is not surprising that Willoughby (1961) found a high diversity and activity of fungi in soils on lake margins. Monchy et al. (2011) observed a high biodiversity in littoral water, and Mohamed & Martiny (2011) found a positive relation of fungal biodiversity to abundance of macrophytes. Nevertheless, fungi are often difficult to recognize due to methodological and morphological considerations: a single observed hypha of one species is visually indistinguishable from a thousand other fungal species. Fungi are highly variable in size and many tend to grow hidden inside their substrates, all factors which make them difficult to study and easy to overlook. The recent and on-going development of modern molecular tools, however, enables ecologists to better resolve biodiversity and ecology of aquatic fungi (e.g. Neubert et al., 2006, Baar et al., 2011). Still, most aquatic plants are only superficially examined for fungi (Orlowska et al., 2004) and many unexplored aquatic microhabitats potentially serve as niches for specialists. Examples include a mutualistic relationship of a predatory *Oomycete* living inside a mussel and protecting the mussel from parasite infections, e.g. nematodes (DeVay, 1956). Another predatory fungus uses the surface structure of macroalgae and grows epiphytically on *Characea* meadows (see figure 5). The most impressive example for interspecies relationships with high impact for general fungal biodiversity considerations stems from members of *Arthropoda.* Theoretically, one single animal can simultaneously provide microhabitats for several aquatic fungi (not including saprophytic or coprophagous fungi): host muscle cells as habitat for intracellular parasites of Microsporidia (Ebert, 1995; Messick et al., 2004); in the host tissue yeasts can be found (Ebert et al., 2004); and in the haemocoel occasionally detrimental *Chytridiomycetes* occur (Johnson et al., 2006). Moreover, an obligate endoparasite of *Entomophthorales* (Sparrow, 1960) and likely a represantative of *Coelomomycetes* (Whisler et al., 1975) can be found and the animal's gut hosts yeasts and symbiotic species of *Harpellales* (trichomycetes; Strongman & White, 2008). Lastly, obligate ectoparasites belonging to an order of higher fungi called *Laboulbeniales* (*Ascomycota)* grow well on the chitinous integument. These fungi are not really aquatic, but more or less specific for arthropods, independent of habitat and are visible on their exoskeletons (Weir, 2004). Interestingly, almost all parasites and symbionts (with the exception of yeasts) are more or less host specific and *Laboulbeniales* are even sex-host specific. If we assume host specificity, a ratio of 6:1 between fungi and their arthropod host species, then a tremendous, yet hidden, fungal biodiversity is implied.

In aquatic microhabitats oxygen conditions can be extremely variable and hence it is important for fungi to be capable of survival or even growth under such conditions. Anoxic conditions are prevalent in aquatic sediments, in animal guts, in biofilms, on decomposing particles or, at a larger scale, in di- to polymictic lakes with seasonally anoxic water masses. Several fungi can withstand anoxic conditions or even grow fermentatively (Held et al., 1969). For example, archaic anoxic environments seem to be predominant habitats for lower fungi and yeasts (Stock et al., 2009; Mohamed & Martiny, 2011) but are awaiting mycologists to explore them.

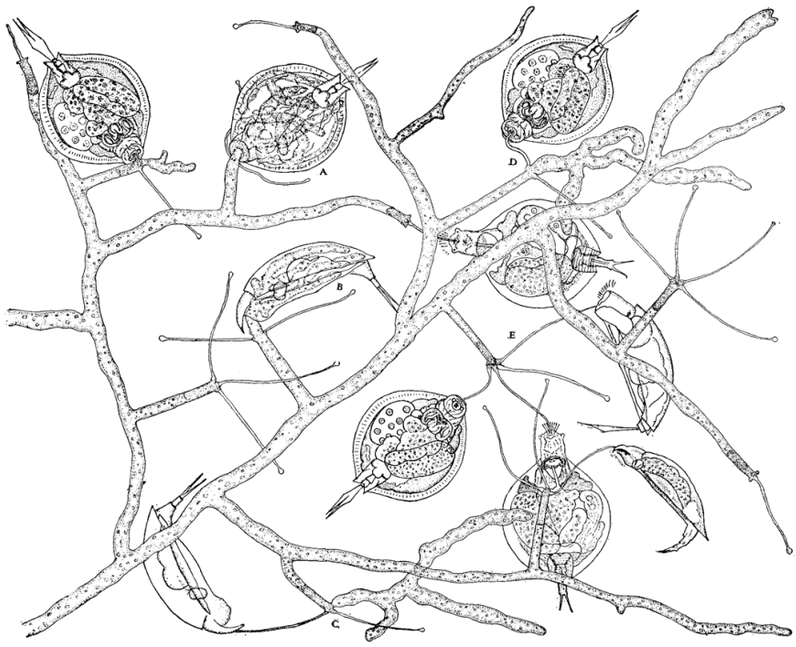

Fig. 5. *Zoophagus tentaclum* captures rotifers and grows epiphytic on *Nitella* (Figure from Karling (1936) with permission).

4. Importance of fungi for aquatic food webs

The importance of fungi as secondary producers of biomass has been well described for headwater streams with leaf litter (Suberkropp, 1992) and for reed stands in littoral zones of lakes and in marshlands. The foregut content of 109 different aquatic insects collected on submerged wood showed that in 66% of all studied insect species fungi were part of their diet (Pereira et al., 1982) and many conidia of aquatic fungi were found in faeces of fish (Sridhar & Sudheep, 2011). Furthermore, it has been shown that food web manipulations greatly alter the fungal biomass in lakes (Mancinelli et al., 2002). This suggests that saprophytic fungi transfer organic matter directly to the higher trophic levels of aquatic food webs. It is therefore likely that environmental change can have severe consequences for overall food web topology, and hence nutrient and energy cycling.

In addition, fungi can be important parasites of primary producers, e.g. phytoplankton, which fuel the aquatic food web with organic matter and energy. Lysis of aquatic organisms by fungal and protozoan parasites increases organic matter and energy cycling. These processes are often solely attributed to *Bacteria* and *Archaea*, however, aquatic fungi actively contribute as mineralisers and parasites.

4.1 Mineralisation

Aquatic systems typically lack effective herbivores meaning that most of the biomass of aquatic macrophytes and riparian plant litter enters the detrital organic matter pool and is subsequently metabolised and transformed into microbial biomass, making it available for higher trophic levels. Generally, a major fraction of carbon will be respired (as CO_2) during degradation, whereas nutrients such as phosphorus and nitrogen are efficiently

recycled. Microbial mineralisation of plant litter supports a complex food-web including all kinds of microbes (*Archaea*, *Bacteria*, fungi, protozoans) and invertebrates (nematodes, trematodes, gammarids, insects, snails). As a consequence plant litter even supplies top predators such as crayfishs, amphibians, birds, fishes and bats with organic matter and energy via the microbial food web. The main basis of the microbial food web consists of fungi and bacteria growing in and on the plant debris. Microorganisms, in particular fungi, possess enzymes capable of degrading even highly polymeric substances, and filamentous fungi are capable of degrading the plant material from the inside, driving the break down of high molecular weight polymers to smaller molecules of medium molecular weight (Fischer et al., 2006). These small fragments and oligomers, e.g. sugar residues, can be readily utilized by bacteria and the so called "sugar fungi" (a sloppy term for the lower fungal phyla consisting of *Chytridiomycota, Blastocladiomycota, Mucoromycotina, Zoopagomycotina, Oomycetes*). Freshwater hyphomycetes of temperate waters are usually well adapted to lower temperatures prevailing during leaf litter input and senescence of aquatic macrophytes. During the cold season (autumn, winter and spring), filamentous fungi account for over 90 to 99% of total microbial biomass in emergent macrophytes and riparian leaf litter and their secondary production is one to two orders of magnitude higher than the bacterial production (Gulis et al., 2009). Therefore, fungal decomposition of this important POM pool seems to be of primary importance during several months in the cold season. Surprisingly, decomposition of submerged aquatic plants has not been well examined, although it is likely that filamentous fungi are of secondary importance (Mille-Lindblom et al., 2006). Thereby, other fungal taxa potentially substitute the filamentous forms, but may vary in time. For example, lower fungi are able to degrade small plant debris and particles. Foremost, *Chytridiomycetes* are suitable candidates since they are able to degrade a wide range of substrates (Sparrow, 1960). However, their saprophytic capabilities and related carbon turnover rates have not been quantified, yet. Some *Chytridiomycetes* can utilise a range of organic polymers such as glucose, starch, sucrose, cellobiose, chitin and cellulose (Gleason et al., 2011; Reisert & Fuller, 1962) whereas others possess incomplete enzymatic degradation pathways suggesting a possible complementation through other microbes. Many active *Chytridiomycetes* often occur sporadically in flooded mud of the riparian zone and submerged sediments and form a very different *Chytridiomycetes* flora compared to that of soils of the catchment area (Willoughby, 1961). This suggests that aquatic *Chytridiomycetes* include indigenous species well adapted to the prevailing environmental factors.

4.1.1 Functional redundancy of saprobes

Lawton and Brown (1993) introduced the concept of functional redundancy as a means of exploring the importance of biodiversity for ecosystem functioning. Functional redundancy is the idea that multiple species can perform the same function within an ecosystem, therefore, a reduction in number of species will not affect ecosystem functioning until all species performing a particular function are lost. However, functional redundancy is at odds with the concept of resource partitioning (Schoener, 1974), which proposes that competition between species drives them to specialise in exploiting discrete resources or ecological niches. Recent research has shown that biodiversity influences aquatic ecosystem processes such as productivity (Smith, 2007; Gustafsson & Boström, 2011) and heterotrophy (Cardinale

et al., 2002), but studies of aquatic fungi show that diversity influences neither productivity (Baldy et al., 2002) nor decomposition rates (Bärlocher & Graça, 2002; Dang et al., 2005). It is likely that both functional redundancy and resource partitioning operate within aquatic ecosystems, but on different spatial and temporal scales, and with impacts at the level of individuals, populations and communities (Loreau, 2004).

In many aquatic ecosystems, saprobic fungi are important decomposer organisms. While some species show a preference for substrates derived from a particular plant species or plant tissue (i.e. leaves or wood), many fungal species are generalist saprobes (Gulis, 2001). This suggests that a large degree of functional redundancy exists among saprobic aquatic fungi at spatial scales ranging from submerged substrates to the whole ecosystem.

Aquatic fungi are microscopic organisms that interact with other species and "individuals" on a microscopic scale via enzymes and biochemical defences. Therefore, resource partitioning by fungi can be expected to occur at the molecular scale. This idea is supported by the well documented temporal succession (Garrett, 1951) that occurs as fungi colonise a submerged leaf, and the temporal partitioning of the resource that is implied. In order to exploit a substrate, fungi secrete extra-cellular enzymes that attack and degrade its chemical constituents. As separate and distinct enzymes or enzyme systems are required for the breakdown of starches, cellulose, hemicellulose, pectin, proteins, lipids and lignin, the fungal species, armed with the suite of enzymes able to efficiently degrade the most labile leaf components, become the initial colonisers. When labile resources are depleted, species able to efficiently degrade the remaining resources become dominant, and so on (Chamier, 1985). Complex plant components such as lignin may be degraded by a range of enzymes secreted by a number of fungal species (Evans et al., 1994), and this is an example of resource partitioning at the sub-molecular level (lignin moieties). It is thus likely that the biodiversity of aquatic fungi has inherent functional redundancy at larger spatial scales, but at the molecular scale, and through time there is inherent functional complementarity, competitive exclusion and resource partitioning.

4.1.2 Fungi as producers of organic matter

There are a number of studies from the past few decades that have established a strong role of fungi as important basal resources in aquatic ecosystems (Bärlocher, 1985; Albariño et al., 2008; Chung & Suberkropp, 2009), most notably in streams (Reid et al., 2008; Hladyz et al., 2009). For example, fungal biomass has been shown to be an important food source for aquatic invertebrates such as snails (McMahon et al., 1974; Newell & Bärlocher, 1993) and insect larvae (Bärlocher, 1981; 1982; 1985). Thereby, the fungal biomass is either removed from the leaf surface, or the leaf itself is consumed.

A synthesis of research from aquatic systems suggests that the functional role of aquatic heterotrophic fungi in moderating the food value of plant detritus may be more important than their role as organic matter producers (e.g. Thorp & Delong, 2002). Litter produced outside a water body may enter the water directly, as a result of abscission from riparian plants overhanging the water body, or may undergo a period of terrestrial aging before entering the water. These two pathways result in differences in litter chemistry (Baldwin, 1999) that influence their importance to the aquatic food-chain (Watkins et al., 2010). In general, fresh plant material has a higher protein content (lower C:N) and a higher proportion of readily available nutrients than aged material (Williams, 2010; Kerr et al., in prep.). However, fresh material also contains inhibitory substances such as tannins, polyphenols and aromatic oils, which function to deter microbial attack and herbivory in the

living plant (Campbell & Fuchshuber, 1995; Canhoto et al., 2002; Graça et al., 2002). In contrast to fresh material, aged organic matter has a higher C:N (low C:N is correlated with higher nutritional value; Boyd & Goodyear, 1971; Hladyz et al., 2009), but a lower content of inhibitory substances.

When fungi colonise submerged plant material that has undergone terrestrial aging, the C:N ratio of the detritus declines (Bärlocher, 1985) as fungi utilise nitrogen from the water column to synthesise proteins for their own growth (Stelzer et al., 2003). They also produce lipids essential for growth (Chung & Suberkropp, 2009) and reproduction (Cargill et al., 1985) in some aquatic invertebrates. In addition to this, the activity of fungal enzymes releases sugars from structural carbohydrates (Chamier, 1985), breaks down lignins reducing leaf toughness (Leonowicz et al., 2001; Medeiros et al., 2009) and neutralises inhibitory substances such as tannins (Mahadevan & Muthukumar, 1980; Abdullah & Taj-Aldeen, 1989). Moreover, where plant detritus undergoes a period of terrestrial or standing dead aging, a more diverse consortium of fungi is able to actively degrade refractory plant components such as lignin (Bergbauer et al., 1992; Abdel-Raheem & Ali, 2004; Schulz & Thormann, 2005). Consequently, the sequential activity of terrestrial and aquatic fungi on plant detritus potentially leads to improved food value for members of the aquatic biota extending from other microorganisms to fish (Williams, 2010).

As aquatic fungi serve as a basal resource in many aquatic ecosystems, it is important to consider factors influencing their productivity. Fungal biomass increases with increasing concentration of nitrogen and phosphorus in the water column (Sridhar & Bärlocher, 1997) and decreases with lower dissolved oxygen concentrations (Medeiros et al., 2009). Thus the productivity of fungi and their importance as organic matter producers vary with climate and the availability of nutrients and organic substrates (Ferreira & Chauvet, 2010), and in some instances fungal production will not be a significant resource for the aquatic community (Bunn & Boon, 1993; Hadwen et al., 2010). Additionally, productivity will also be limited by ecological interactions such as competition (Mille-Lindblom et al., 2006) and mycotrophy (Newell & Bärlocher, 1993; Kagami et al., 2004; Lepere et al., 2007), and physical changes such as burial (Janssen & Walker, 1999; Cornut et al., 2010).

4.2 Parasites

Fungal pelagic parasites are often host-specific, but their evolution didn't stop at the species level and several fungal species developed dependencies on (1) certain algal cell types, e.g. heterocysts and akinetes (Sparrow, 1960); (2) certain cell entry sites of the host cell (Powell, 1993); and (3) certain algal strains (De Bruin et al., 2008). The latter study targets a prominent freshwater diatom called *Asterionella formosa* because it often harbours a obligatory, host-specific, very virulent fungal parasite called *Zygorhizidium planktonicum*. Infection by this fungus is often epidemic and can rapidly reach up to 90% of the host population with fatal consequences for the host. Interestingly, the authors could show that a genetically diverse host population maintains an evolutionary equilibrium between the parasite and the host population. A diminished host diversity, which is promoted, e.g. by disturbance or algal monoculture, would allow a rapid adaptive evolution of the parasite with a serious aftermath.

The occurrence of hyperparasites is really amazing since such fungi represent parasites of the algae's fungal parasites. Examples of these hyperparasites of fungal parasites on *Cyclotella, Cosmarium and Asterionella* are given by Canter-Lund & Lund (1995). Fungal

hyperparasites belong to the genus *Rozella.* This genus was formerly assigned to the *Chytridiomycetes* and is now proposed to be part of the unique fungal phylum of the Rozellida (Lara et al., 2010). All members of *Rozella* are considered to be parasites of lower fungi (*Chytridiomycetes, Blastocladiomycetes, Oomycetes*). It is intriguing to think about the minimum population size of parasitic/saprobic fungi needed to sustain an obligate mycoparasitic fungal population. This suggests that a very common and stable mycoplankton population must exist in aquatic systems. Therefore, parasitism can be regarded as a key driver of food-web stability and POM transfer.

4.3 Stabilisation of ecosystems

As shown above, fungi possess multiple ecological functions in aquatic food webs. They often have a dual role which is on the one hand consumption of organic matter and on the other hand transmission of energy and genetic information (Amundsen et al., 2009; Rasconi et al., 2011). Parasitic fungi, for example, can selectively alter food web topology and thereby increase interactions and nestedness of ecosystems. Parasites including fungi, for example, interlink organisms of all trophic levels (resulting in twice as many links as without parasites) and thus increase food chain length and number of trophic levels. Amundsen et al. (2009) show that 50% of all parasites are trophically transmitted and thereby exploit different trophic levels and largely increase omnivory in the trophic web. They also show that the number of trophically transmitted parasite-host links is positively correlated with the linkage density of the host species, i.e. highly connected species have a higher rate of infection, in particular those with complex life cycles. Therefore, parasites play a prominent role in ecological networks, significantly increasing interaction strength and hence selectively changing food web links.

Parasites are ubiquitous in the aquatic environment and have subtle, sublethal or even lethal impacts. Their impacts on hosts are propagated up and down food webs and thus are manifested throughout the entire community. Environmental changes, however, greatly affect their dynamics and hence parasites can be seen as indicators of many aspects of host physiology. Parasites are uniquely situated within food webs, and following their transmission process could serve management and ecosystem conservation (Marcogliese, 2004; Lafferty et al., 2006). In general, the diversity of parasites reflects the overall diversity within the ecosystem (see Rasconi et al., 2011). In many pelagic systems, fungal parasites are 1) a driver of phytoplankton community structure, 2) crucial for organic matter and energy transfer, 3) important for food web dynamics by affecting fitness and reproduction of many aquatic organisms and 4) causes of intra-specific variability and even increased speciation. Since fungal parasites largely increase the number of trophic levels and often lower the dominance of a few species they also increase ecosystem stability and most likely even functional diversity. Fungi are also potential vectors of genetic elements and hence may also transfer genetic information between organisms of different trophic levels. In any case, they lead to a higher biodiversity by affecting key evolutionary parameters and also functional diversity, e.g. by transferring terrestrial material including leaves and pollen - otherwise unavailable for aquatic organisms - to higher trophic levels (e.g. Masclaux et al. 2011). Hence, aquatic fungi should be seen as key variables for food web structure and genetic as well functional diversity of the aquatic community rendering it less susceptible to changes in environmental variables.

5. Assessing fungal biodiversity and functionality in aquatic ecosystems

Next to classical molecular techniques for assessing *in situ* fungal communities (Bärlocher 2007), massive parallel DNA sequencing in combination with data management systems such as GenBank (Benson et al., 2008), it is now possible to fully explore fungal biodiversity. Amplicon sequencing has been used to explore fungal diversity in soils (Buée et al., 2009; Lim et al., 2010). The approach was recently used in an assessment of estuarine biodiversity (Chariton et al., 2010) and for the first time in two lakes (Monchy et al., 2011), and similar work from a lowland river floodplain has not been published to date (Colloff & Baldwin in prep; Kerr et al., in prep.).

These studies greatly extend our understanding of dimensions and structure of the fungal kingdom. However, in many cases, all we know of newly discovered species is the sequence of a small part of their genome, with no insights regarding morphology, physiology or ecology of the specimen. In the future, a combination of techniques such as transcriptomics (Bhadauria et al., 2007), proteomics (Doyle 2011), metabolomics (Tan et al., 2009) may allow us to evaluate physiological and ecological inferences based on DNA sequences. Classical culture techniques, however, will remain important for studying morphology, preserving voucher specimens, and generally expanding our knowledge of undescribed species associated with novel sequences.

At present, there are a number of biases in the representation of described species in databases such as GenBank. For practical reasons, investigations have focused on the ecology and diversity of macro-fungi and pathogens of plants and animals. In order to use DNA sequence databases to identify fungi in environmental samples, it is at first necessary to fill the database with accurate and appropriate information on fungal sequences with taxonomic descriptions. It is unlikely that this work can keep pace with the potential of current technologies to generate sequence data. Nevertheless, improved sequence analysis techniques are required to link information of the "omics" studies with those of the environment including short- and long-term changes. Although identification of fungi in the environment has been improved a lot throughout the past years, there is an obvious lack in fundamental ecological methods, e.g. methods for differentiating between the biomass of fungal species are still needed. FISH methods, which allow determining fungal biomass have only recently emerged (Mangot et al., 2009) and ergosterol measurements are only applicable to CPOM where algae are not present (e.g. *Chlorella* – a typical fresh water alga - contains ergosterol) and can't detect the presence of many species of lower fungi. To understand the importance of fungi for energy and organic matter cycling in aquatic systems, we need to greatly improve our techniques, e.g. by defining new marker molecules to measure the biomass and activity of fungi in their natural environment.

6. Concluding remarks

Present estimations suggest that global fungal diversity greatly exceeds that of any other group of microbes. As documented above, their function is of global importance for nutrient cycling and ecosystem health. For example, networks of fungal hyphae interconnect a whole habitat and trigger the transport of macro- and micronutrients over large distances to other heterotrophic microbes (Harms et al., 2011). Aquatic habitats are no exceptions in this respect and the loss of fungi severely affects aquatic food web topology and hence

functioning (Lafferty et al., 2008). Hypothetical scenarios resulting from the loss of fungal diversity include: aggradation of aquatic ecosystems via the accumulation of CPOM and polymers, a decline in macroinvertebrate food sources, a reduction in the rate and range of decontamination of industrial toxins, diminished total diversity in planktonic communities and the development of fungal monocultures that would potentially impact on total biodiversity. Since fungal biodiversity is representative of ecosystem functioning and thus of ecosystem health, it is in the interests of human society to explore the fungal biodiversity present in natural environments, especially aquatic habitats.

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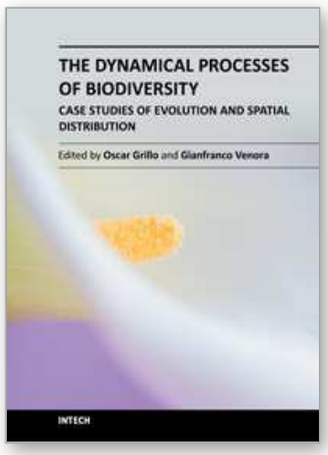

The Dynamical Processes of Biodiversity - Case Studies of Evolution and Spatial Distribution

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Driven by the increasing necessity to define the biological diversity frame of widespread, endemic and threatened species, as well as by the stimulating chance to describe new species, the study of the evolutive and spatial dynamics is in constant execution. Systematic overviews, biogeographic and phylogenic backgrounds, species composition and distribution in restricted areas are focal topics of the 15 interesting independent chapters collected in this book, chosen to offer to the reader an overall view of the present condition in which our planet is.

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